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Attending to Features inside and outside the Spotlight of Attention

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Previous studies in monkeys and humans have revealed neural correlates and perceptual consequences of feature-based attention. In this issue of *Neuron*, two brain-imaging studies from Serences and Boynton and Liu et al. bridge the gap between single neurons and behavior by demonstrating a highly functional attention system that acts on neural representations of our visual world enhancing the processing of the currently attended set of features at the expense of information about less relevant aspects.

Attention has long been recognized as a powerful influence on perception. It endows us with the ability to selectively modulate sensory information processing based on the behavioral relevance of signals picked up by our sensors. In the visual domain, most research has focused on spatial attention, i.e., the attentional selection based on the current region of interest in the visual field. Across visual cortex, neural correlates of spatial attention have been demonstrated, most prominently in the enhanced response of neurons whose receptive fields overlap the current spatial focus of attention (Womelsdorf et al., 2006). The prominent retinotopy of many visual cortical areas in primates has allowed functional brain-imaging studies in humans to visualize this "spotlight" of attention as a focal region of enhanced activity, matching the predictions based on the findings from single-cell recording studies in monkeys.

However, attention can be allocated not only to a particular region of space, but also to a visual feature, such as a particular color or direction of motion. Recordings from monkey visual cortex have demonstrated neural correlates of this type of attention in both the ventral and dorsal visual pathway (Maunsell and Treue, 2006). Because of the similarity of some of the neuronal characteristics of feature-based and spatial attention and because the spatial location of a stimulus might be considered just another feature, it has been suggested that rather than being a distinct mechanism, feature-based attention might rely on mechanisms closely related to the ones being used by spatial attention. The most prominent neural effect of feature-based attention is a global enhancement of responses from neurons selectively tuned to the attended feature and a corresponding suppression of the opposite feature (Treue and Martinez-Trujillo, 1999), i.e., attending to upward motion at one location in the visual field leads to an enhanced response in neurons selective for upward motion even when their receptive fields are far away from the attended location. These gain changes create a nonmultiplicative enhancement of the selectivity of the population response that emphasizes the attended over the unattended feature (Martinez-Trujillo and Treue, 2004).

Correspondingly, psychophysical studies have shown that feature-based attention enhances behavioral performance for the attended feature across the visual field. This specific enhancement makes feature-based attention particularly useful in visual search since it will highlight those regions of the visual scene containing the searched-for features. Figure 1 illustrates this effect, i.e., when searching for a person wearing a red shirt within a crowd (Figure 1, left) the brain highlights regions containing the color red (Figure 1, right) while suppressing other image regions, creating a scene representation shaped by the behavioral context.

Even though several nonspatial features (e.g., orientation and direction of motion) have been show by single-cell recording studies in primate cortex to be topographically organized, feature-based attention has mostly been out of reach of imaging approaches since the respective topography is microscopic, i.e., the clustering of neurons preferring similar features occurs at a spatial scale beyond the resolution of today's scanners. It has been the development of pattern classification algorithms, an ingenious analysis technique that can detect specific activation of highly interdigitated cortical representations that has allowed studying aspects of feature-based attention across multiple areas in human visual cortex.

Serences and Boynton (2007) (this issue of *Neuron*) presented human subjects with two stimuli placed left and right of a fixation point on a visual display. Each stimulus appeared as two surfaces sliding transparently across each other because it was created by the superposition of two random dot patterns, one moving up and to the left and the other up and to the right. During a given block of trials, subjects were instructed to attend to one of the four moving surfaces. The authors recorded blood oxygenation level-dependent (BOLD) signals in

Figure 1. Illustration of the Effect of Feature-Based Attention (Here Searching for a Person with a Red Shirt)

visually responsive regions of occipital, parietal, and frontal cortex. Using a pattern classification analysis, they were able to demonstrate that allocating attention to one or the other of the two superimposed surfaces in one stimulus produces a different pattern of activation across visual areas, i.e., when evaluating a given pattern, the authors were able to recover which motion direction the subject was currently attending to, both for cortical regions representing the attended as well as for regions representing the unattended stimulus. This clearly shows that attending to a particular direction in one location of the visual field specifically modulates direction-selective units across the visual field. This signature of feature-based attention was present in the unattended hemifield even during trials where the unattended stimulus was not shown. This is an important aspect, as it rules out the alternate possibility that a feature-specific enhancement of an irrelevant stimulus reflects a perceptual "tagging" of this distractor caused by this distractor's matched feature rather than a stimulus-independent feature-specific gain change in the neuronal population (Saenz et al., 2002). This observation that the direct effect of feature-based attention targets neuronal sensitivity rather than stimulus representations nicely parallels similar findings in the realm of spatial attention where response modulation has also been observed in the absence of visual stimuli in the receptive field (Luck et al., 1997).

An interesting observation in the Serences and Boynton (2007) study is the feature-specific attentional signal they observed in the frontal eye fields (FEF) and the inferior parietal sulcus, areas less associated with directional tuning than the earlier visual areas. This suggests that particularly the FEF, which has been linked to spatial attention (Moore et al., 2003) might also contain relevant signals for the control of feature-based attention.

The study of Serences and Boynton (2007) focuses on motion stimuli, areas of the dorsal visual-processing pathway, and the effects of feature-based attention outside the spatial spotlight. A study by Liu et al. (2007) (this issue of *Neuron*) applies a combination of psychophysics and functional imaging to investigate the selective power, perceptual consequences, and neural basis of feature-based attention at the location of spatial attention. The authors use a visual illusion, the tilt aftereffect (TAE), to show that in human visual cortex, attended features create stronger aftereffects. The classical TAE depends on the adaptation with one orientation. Instead, Liu et al. (2007) used two superimposed orientations, and the subjects' attention was directed to one of them. As in similar psychophysical studies (e.g., Lankheet and Verstraten, 1995), the aftereffect reflected the attended orientation, indicating that feature-based attention strengthened the corresponding orientation component and consequently affected the tilt aftereffect. Liu et al.'s study goes beyond these psychophysical observations by demonstrating that the fMRI response to a single orientation after it had been the attended one during a preceding adaptation phase with two orientations was similarly reduced in several visual areas (V1, V2, V3, V3A/B, hV4, LO1, and V7). Furthermore, subjects showed a correlation between the magnitude of the TAE and the fMRI response to an unattended orientation in area V1. These findings extend the fMRI evidence for the presence of feature-based attention by demonstrating it inside the multiple representation of the spotlight of attention across visual cortex.

Together, the two studies of feature-based attention in human visual cortex in this issue help to bridge the gap between previous electrophysiological recordings in awake monkeys and studies of human perception by using functional imaging, behavioral measurements, and computer modeling to investigate the underpinning of feature-based attention in human visual cortex. The results demonstrate a highly functional attention system evolved to create a neural representation of our visual environment that enhances regions and objects resembling the currently attended set of features at the expense of information about less relevant aspects. This system is unaffected by spatial attention, i.e., it operates both within and outside the current spotlight of attention.

Not surprisingly, the studies also raise important questions and provide

pointers for future research. Most prominently, a notable gap in our understanding of feature-based attention exists as to from where and how its allocation is controlled. While the FEF is an appealing possibility, the dorsolateral prefrontal cortex, which builds representations of learned visual features or objects (Funahashi, 2006) might also play a role. Similarly the integration of the various types of attention identified so far (e.g., spatial, feature-based, surface-based, object-based, etc.) at the level of single neurons requires more research.

The excellent agreement between the new functional imaging data from human cortex with the result of previous electrophysiological recordings from single cells in monkey cortex nicely demonstrates how both approaches inform each other and how true progress in modern neuroscience depends on an integrative approach harnessing the abilities of a broad range of techniques. Future progress on the open questions most likely will depend on just such an approach.

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Enigmas of the Dentate Gyrus

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We are rapidly approaching a better understanding of the mechanisms that allow our brains to form distinct representations for similar events or episodes. McHugh et al. have brought that goal one step closer by showing that NMDA receptor-dependent synaptic plasticity in the dentate gyrus is necessary for immediate differentiation between environments with similar features.

How does the brain distinguish between memories that are similar, such as this year's birthday compared to last year's? How do you remember that Kristin helped your daughter open presents during her garden party when she became 4, whereas it was Erika who had that job when she turned 5 (Figure 1)? The hippocampus, a key structure involved in the storage of episodic and declarative memories (Tulving and Markowitsch, 1998; Squire et al., 2004), may have just the properties required to deal with these challenges.

A critical step in the encoding of a new episodic memory is the amplification of the differences between the new representation and representations that already exist in the network, a process termed "pattern separation." Lesion studies in behaving rodents have suggested that a neuronal pattern-separation mechanism may be located within a subregion of the hippocampal formation, more specifically in the granule cell population of the dentate gyrus (Rolls and Kesner, 2006). This interpretation has been supported by studies of place cells in the hippocampus. Place cells signal the animal's location by firing specifically when the animal is in a specific part of the environment (O'Keefe and Dostrovsky, 1971). One well-characterized feature of these cells is their tendency to substantially change their firing patterns after only minor changes in the sensory input or the motivational context, a phenomenon referred to as "remapping" (Muller et al., 1991). Studies of remapping have provided important clues to the neuronal network mechanisms for pattern separation. Two forms of remapping have been identified in the CA3-dentate network of the hippocampus (Leutgeb et al., 2005, 2007). During "global remapping," there is a complete redistribution of both firing locations and firing rates in the cell population. This form of remapping is invariably associated with a shift in the spatial inputs from the entorhinal cortex (Fyhn et al., 2007). During "rate remapping," only the rates of the active hippocampal cells change